

# A Study of Variation in Eastern Timber Rattlesnakes, *Crotalus horridus* Linnae (Serpentes: Viperidae)

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**ABSTRACT.**— Variation was examined in specimens of *Crotalus horridus* from the eastern United States in an attempt to investigate the status of its two described subspecies, *C. h. horridus* and *C. h. atricaudatus*, as defined by Gloyd. A particular effort was made to duplicate the results of a study by Pisani, Collins, and Edwards, who concluded that the subspecies were invalid. Maximum likelihood factor analysis and step-wise discriminant analysis on the same morphological characters, plus several others relating to adult size and pattern, produced evidence that the two subspecies of *C. horridus* are valid in the eastern portion of its range. However, standard morphological characters alone are not sufficient to discriminate between the two forms. Rather, adult size and pattern differences, in conjunction with the number of dorsal scale rows and ventral scales, best differentiate *C. h. horridus* from *C. h. atricaudatus*.

Two subspecies of the rattlesnake *Crotalus horridus* are thought to occur in the eastern United States (Conant 1975): *C. h. horridus*, the timber rattlesnake, and *C. h. atricaudatus*, the canebrake rattlesnake. Gloyd (1940) defined the former as having 23 dorsal scale rows, a lower number of ventral and caudal scales, an absent or faint postocular stripe, and less brilliant contrast between the ground color and pattern. He defined the latter as having 25 dorsal scale rows, a higher number of ventral and caudal scales, larger size, and more brilliant markings. The geographic range of the two races is shown in Figure 1.

*Crotalus horridus* shows considerable variation in the western portion of its range; *C. h. atricaudatus* is not known to occur in Oklahoma, yet specimens of *C. h. horridus* from southeastern Oklahoma resemble *C. h. atricaudatus* in color and pattern (Webb 1970). Anderson (1965) found that populations of *C. h. horridus* from western Missouri possessed a reddish-brown middorsal stripe like that of *C. h. atricaudatus* from southeastern Missouri. Gloyd (1940:186) also reported that "the middorsal stripe of reddish brown, although very conspicuous in typical (*C. h. atricaudatus*) specimens, is not a good definitive character because of its common occurrence in specimens of *C. h. horridus* from western localities." Smith (1961) regarded Illinois specimens from Jackson

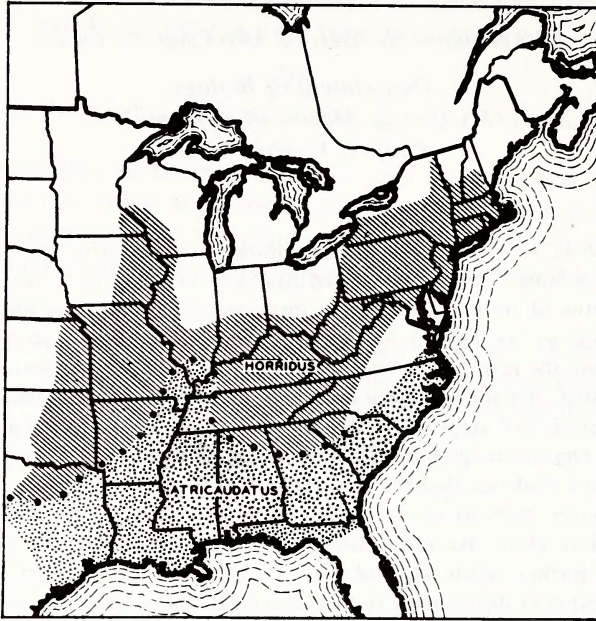


Fig. 1. Range of *Crotalus horridus* (from Klauber 1972).

County and southward as intergrades, because the specimens of *atricaudatus* from counties bordering the Mississippi River more closely resembled *horridus* in some characters.

A study by Pisani et al. (1973) concluded that, on the basis of 13 morphological characters, the recognition of subspecies in *C. horridus* could not be justified. They examined specimens from localities throughout the range, including western populations where intergradation is thought to occur.

The purpose of this study was to examine variation in pattern and adult size differences in addition to those morphological characters used by Pisani et al. (1973) in eastern *C. horridus* to determine if a more comprehensive study of the species is needed.

#### MATERIALS AND METHODS

Data were obtained on 337 museum specimens from New Hampshire, Vermont, Massachusetts, Connecticut, New York, New Jersey, Pennsylvania, Maryland, Virginia, North Carolina, South Carolina, Georgia, and Florida. However, only 101 specimens were suitable for the analyses used here in that they were complete in all characters examined. Twenty-one specimens were from localities of probable intergradation, and so were treated separately. Of the remaining 80, 10 were juveniles and were eliminated from some analyses. Localities of the 101 specimens used are shown in Figure 2. The characters used in this study

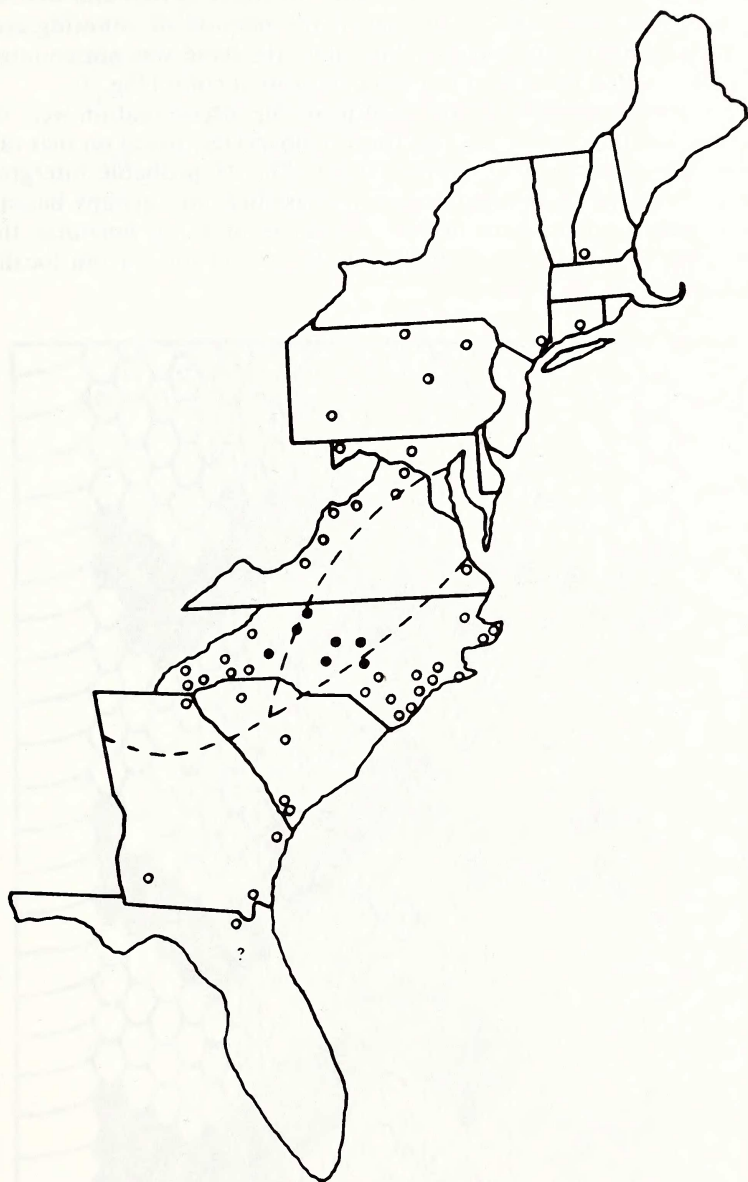


Fig. 2. Localities of specimens used in this study. Each circle represents at least one *Crotalus horridus*. Solid circles represent specimens from localities of probable intergradation. A question mark indicates an unknown locality for the state. Dashed lines are approximate range limits for each subspecies (see Fig. 1).

are listed in Table 1; the first 13 are those of Gloyd (1940) and were also used by Pisani et al. (1973). However, the method of counting crossbands was probably different in this study; the band was not counted if it was interrupted by at least one scale of ground color (Fig. 3).

Specimens not from localities of probable intergradation were classified *a priori* into one of the two forms (subspecies) based on that race's distribution as defined by Gloyd (1940). The 21 probable intergrades (Fig. 2) not used in the analyses were classified into groups based on their localities: those from within the range of *C. h. horridus*, those from within the range of *C. h. atricaudatus*, and those from localities lying between the two ranges.

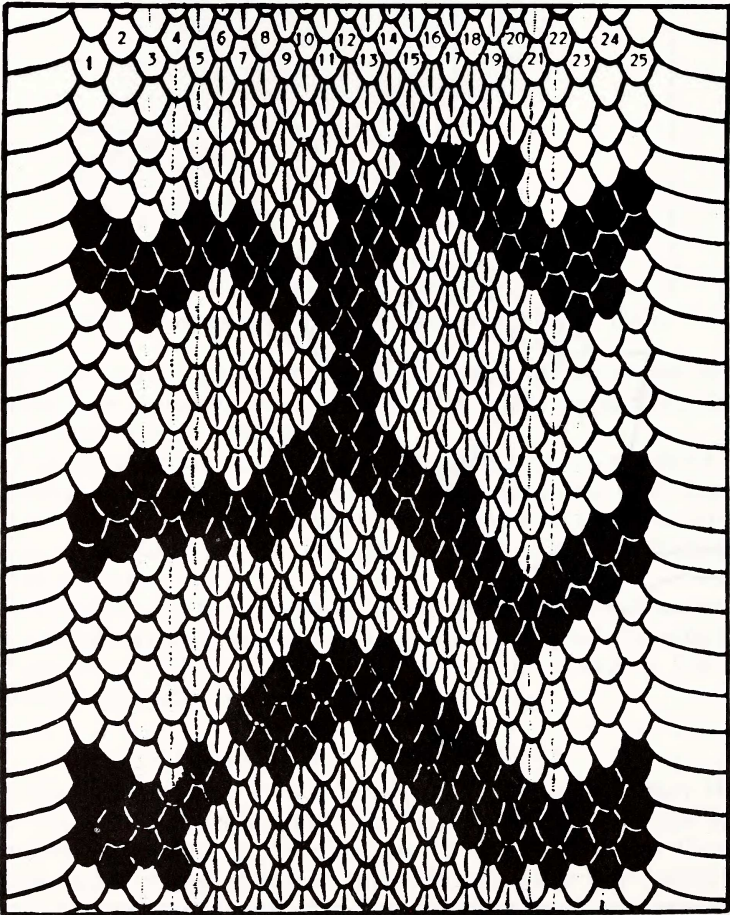


Fig. 3. Method of counting dorsal scale rows (numbered at top) and crossbands. Of the three apparent bands, only one complete crossband would be counted here, for only one is uninterrupted by any scales of ground color.

Table 1. Characters examined in this study of variation in *Crotalus horridus*. The first 13 were used by Pisani et al. (1973).

No.	Character	Description
1	ADS	Anterior dorsal scale rows, counted at one head-length posterior to the occipit (see Fig. 3).
2	DSM	Dorsal scale rows at midbody.
3	PDS	Posterior dorsal scale rows at one head-length anterior to the anal plate.
4	VS	Number of ventral scales, not including the anal plate (Dowling 1951). This method was not used by Pisani et al. (1973).
5	CS	Number of caudal scales, starting with the first complete scale posterior to the anal plate.
6	DCS	Number of divided caudal scales.
7	LSL	Left supralabials.
8	RSL	Right supralabials.
9	LIL	Left infralabials.
10	RIL	Right infralabials.
11	BCB	Number of complete body crossbands, counted between the head and anal plate (Fig. 3). This is not the method used by Pisani et al. (1973), who were not sufficiently clear on how crossbands were distinguished from blotches.
12	TCB	Number of complete tail crossbands. Although many specimens possessed tail markings that suggested banding, relatively few had tail crossbands that were clearly entire. Most specimens had a dark-colored tail with no markings, the dark color extending well anterior to the vent.
13	R	Ratio of tail length to snout-vent length. Tail length was measured from the posterior margin of the anal plate to the base of the first rattle segment.
14	SVL	Adult snout-vent length. Individuals longer than 750 mm were considered adults, but this may have failed to exclude a few sub-adults.
15	TL	Adult tail length.
16	HL	Adult head length, measured from tip of rostrum to line joining posterior tips of mandible (Peters 1964).
17	MS	Middorsal stripe, coded as zero for either faint or completely absent and as one for clearly present.
18	GC	Ground color, an attempt to measure pattern contrast. Because many museum specimens had lost some of their original color, this was coded as either zero to denote light colors, such as pale brown, tan, pinkish, yellowish, and pale gray, or as one to denote dark colors, such as plain brown, dark gray, and dark olive-greenish. Some melanistic specimens were examined, but none were used in the analyses because they lacked other essential characters.
19	POS	Postocular stripe, coded as zero for absent or faint and as one for clearly present on one or both sides of the head.

Table 2. Results of factor analyses. The first analysis was performed on the 13 morphological characters used by Pisani et al. (1973); all 19 characters were used in the second analysis.

	Factor 1		Factor 2		Factor 3		Factor 4	
	First analysis	Second analysis	First analysis	Second analysis	First analysis	Second analysis	First analysis	Second analysis
Eigenvalue	2.194	3.089	1.677	2.987	1.474	2.334	1.433	1.385
Cumulative proportion of total variance	0.15	0.20	0.24	0.36	0.40	0.42	0.52	0.52
Factor loadings (and characters)	0.922 (R)	0.973 (SVL)	0.743 (DSM)	0.966 (R)	0.977 (RIL)	0.844 (ADS)	0.997 (LSL)	0.836 (MS)
	0.866 (CS)	0.891 (HL)	0.734 (ADS)	0.861 (CS)		0.609 (DSM)	0.557 (RSL)	
		0.572 (TL)		0.796 (TL)				
		0.509 (POS)						

Table 3. Results of discriminant analyses. The first analysis was performed on the 13 characters used by Pisani et al. (1973); all 19 characters were used in the second analysis.

	First analysis	Second analysis
Number of variables in discriminant function	5	4
Eigenvalue	1.088	2.989
Wilks' lambda	0.479	0.251
Approximate F-value (P = 0.01)	16.103	48.577
Canonical correlation	0.722	0.866
Coefficients for canonical variable	-0.156 (BCB)	-0.109 (HL)
	-0.216 (VS)	-0.119 (VS)
	-0.346 (TCB)	-0.376 (ADS)
	-0.419 (DSM)	-2.217 (MS)
	-0.514 (PDS)	
Constant	57.593	35.626

A maximum likelihood factor analysis (Dixon and Brown 1979), in which all variables are evaluated simultaneously, was employed primarily to determine the existence of groups that correspond to subspecies. Two factor analyses were conducted, first on the 13 morphological characters used by Pisani et al. (1973), and then on all 19 characters. To analyze group integrity, we used stepwise discriminant analysis, which, like the factor analysis, evaluates all variables simultaneously (Dixon and Brown 1979). Again, two discriminant analyses were conducted, one on the characters used by Pisani et al. (1973) and one on all 19.

The maximum number of discriminant functions to be derived in a one discriminant analysis is either less than the number of groups or the same as the number of discriminating variables, whichever is smaller (Nie et al. 1975). Because there are only two groups in this study, there is only one discriminant function. Three criteria for evaluating this function are the eigenvalue, canonical correlation, and Wilks' lambda. The eigenvalue is a measure of the total variance explained by the discriminating characters. The canonical correlation is a second measure of the function's ability to discriminate among the groups. Wilks' lambda is an inverse measure of the discriminating power in the characters that have not been removed by the discriminant function. A smaller lambda, then, means more information is accounted for in the discriminant function. In Biomedical Computer Programs (BMDP), the Wilks' lambda is transformed into an approximate F-value.

Since there is one discriminant function, there can only be one canonical variable, which is the linear combination of variables entered that best discriminates among the groups (the largest one-way ANOVA F-value) (Dixon and Brown 1979). The canonical variable is adjusted so that the pooled within-group variance is one, and its overall mean is

zero. The canonical variable is then evaluated at the group mean for each specimen, and all cases are plotted in a histogram to demonstrate separation of distinct groups. Table 3 lists the constant and canonical coefficients of the discriminating characters for each analysis. Figure 6 shows a comparison of the histogram from each discriminant analysis.

Analysis was performed at the George Mason University Computing Services on the Cyber 170-720 computer system. The P-series of the BMDP (Dixon and Brown 1979) was used, as were all default procedures, except the second factor analysis, in which four factors were requested.

#### *Specimens Examined:*

Carnegie Museum (CM): S 9130; 36497, 40186, 40187, 40192, 54721, 91446, 91447, 91482-91484, 91582, 91583, 91677, 92053, 92056, 92057, 92063, 92065

North Carolina State Museum (NCSM): 2347, 5744, 8035, 8041, 8121, 8520, 8725, 9638, 9655, 9772, 9879-9885, 9888, 10229, 10779, 10920, 11017, 11259, 11874, 11875, 12011, 12061, 12108, 12112, 12113, 12263, 12266, 12795, 12857, 12894, 12911, 13899, 14011, 14111, 14141, 15678, 15793, 15926, 16657, 16711, 17056, 17059, 17105, 17150, 19241, 19359, 19595, 19641, 21808

National Museum of Natural History (USNM): 8372, 9973, 10519, 14755 (2 specimens), 17959, 19970, 20651, 29362, 44313, 49958, 101858, 102714, 107879, 108687, 110487, 127601, 129094, 129759, 130167, 130168, 139618-139620, 145377, 156804, 210092, 218911.

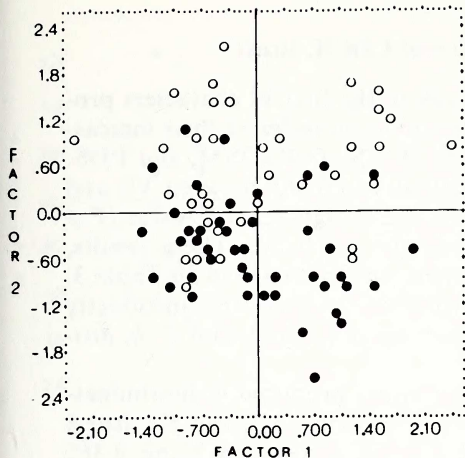
## RESULTS

Four factors accounting for 52% of the variance were produced in the factor analysis of the first 13 characters. The variation in characters CS and R correlated most closely with factor 1; ADS and DSM with factor 2; RIL with factor 3; and LSL, RSL with factor 4. Character variation that correlated less than 0.500 with any factor was not considered significant. The factor loadings and eigenvalues are summarized in Table 2, and estimated factor scores for the 80 specimens used are plotted in Figure 4.

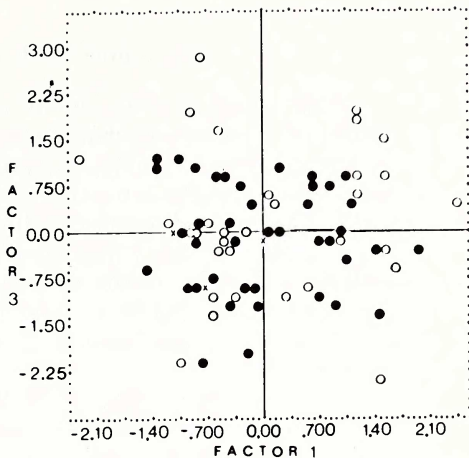
In the factor analysis of all 19 characters, 4 factors were requested to limit the number produced. These accounted for a cumulation of 52% of the variance, but the characters SVL, TL, HL, and POS correlated most closely with factor 1; CS, R, and TL with factor 2; ADS and DSM with factor 3; and MS with factor 4. These results are summarized in Table 2. Factor scores for the 70 specimens used are plotted in Figure 5.

Fig. 4. Scatterplots of estimated factor scores for specimens from the factor analysis of the first 13 characters. Solid circles represent one or more specimens of *Crotalus h. horridus*; open circles represent specimens of *C. h. atricaudatus*. Tail measurements (characters CS and R) correlated most closely with factor 1; dorsal scale rows (ADS and DSM) correlated with factor 2; infralabials (RIL) correlated with factor 3; and supralabials (LSL and RSL) correlated with factor 4.

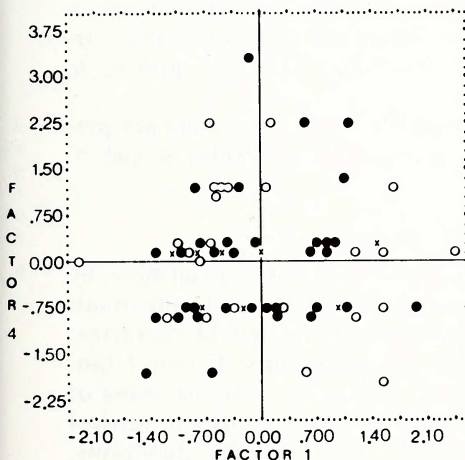




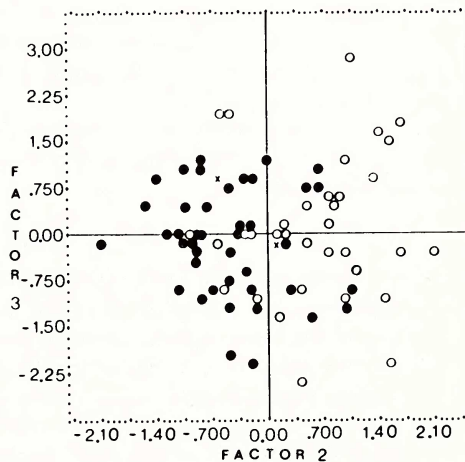
A



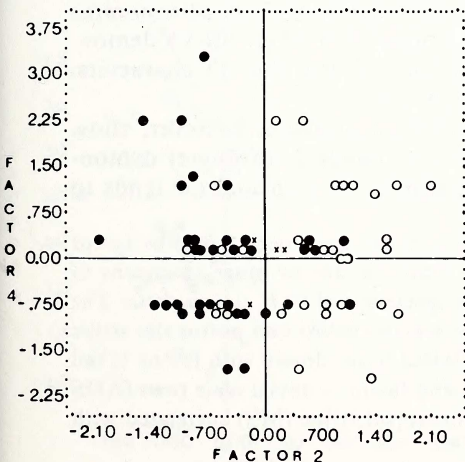
B



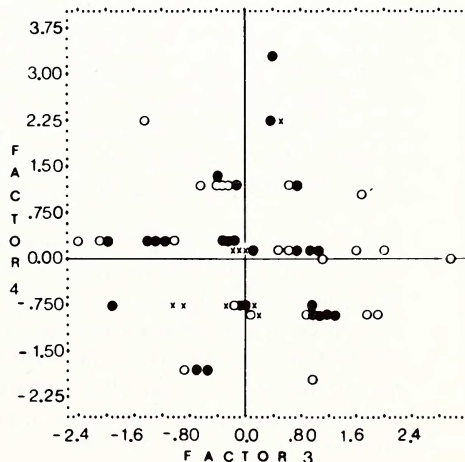
C



D



E



F

Initial stepwise discriminant analysis of the first 13 characters produced 5 discriminating characters. They were, in order of their increasing ability to discriminate, characters BCB, VS, TCB, DSM, and PDS. None were strongly correlated; the highest was 0.365 between VS and DSM. The single discriminant function had a significant F-value ( $P = 0.01$ ) of 16.103 and a canonical correlation of 0.722. These results, including the value of the Wilks' lambda, are summarized in Table 3. Thirteen (16%) of the 80 specimens used in this analysis were incorrectly classified into the two groups: *C. h. horridus*, 6 (13.6%), and *C. h. atricaudatus*, 7 (19.4%).

Discriminant analysis of all 19 characters produced 4 discriminating characters: MS, ADS, HL, and VS. Characters MS and HL had a weak correlation of 0.633, the next highest correlation being 0.366 between HL and VS. The discriminant function had a significant F-value ( $P = 0.01$ ) of 48.577 and a canonical correlation of 0.866. These results, including the value of the Wilks' lambda, are summarized in Table 3. Five (7%) of the 70 specimens used in this analysis were incorrectly classified into the groups: *C. h. horridus*, 4 (11.1%), and *C. h. atricaudatus*, 1 (2.9%).

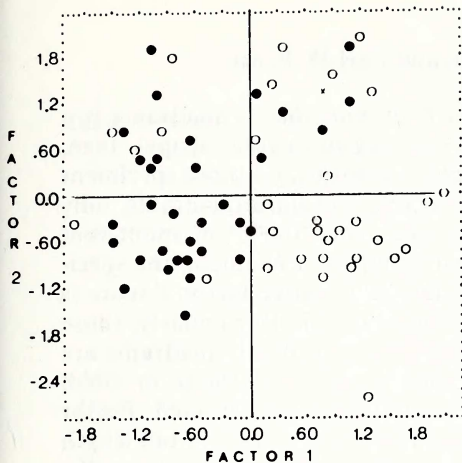
Group means and standard deviations of all 19 characters are presented for both nonintergrades and intergrades in Tables 4 and 5, respectively.

## DISCUSSION

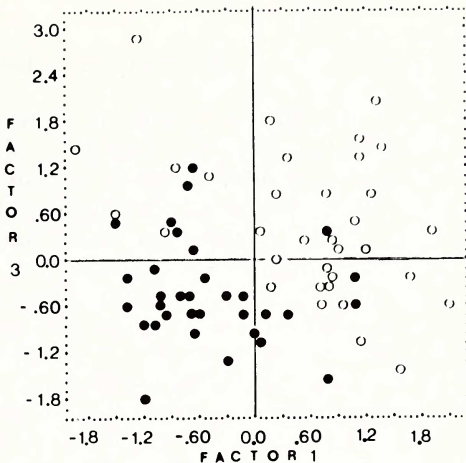
One purpose of the factor analysis performed was to determine, by inspection of the plotted factor scores, whether clusters of individuals occur that correspond to subspecies. Analysis of the first 13 characters reveals little or no clustering in any of the scatterplots. Factor 1 (abscissa) versus factor 2 (ordinate) appears to have the best clustering of the six graphs (Fig. 4A). Separation seems to occur along the vertical axis. *Crotalus h. atricaudatus* tends to cluster in the first two quadrants, while *C. h. horridus* tends to cluster in quadrants three and four, indicating separation on the basis of dorsal scale rows (factor 2). However, overlap is wide. More than 25% of the specimens of *C. h. atricaudatus* lie below the first two quadrants. No other plot (Fig. 4B-F) demonstrates any distinct clustering. On the basis of the first 13 characters, therefore, no subspeciation can be recognized.

The plots from the analysis of all 19 characters, however, show contrary results. Factor 1 (abscissa) versus factor 2 (ordinate) demonstrates clustering along the horizontal axis: *C. h. atricaudatus* tends to

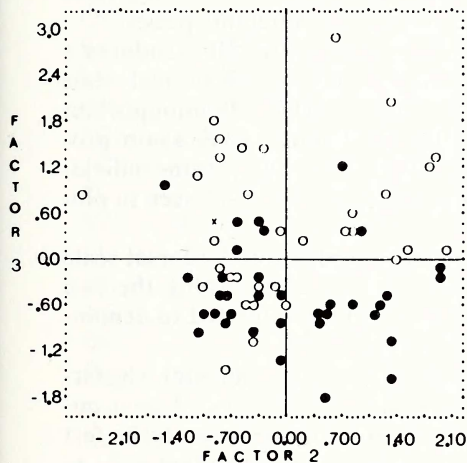
Fig. 5. Scatterplots of estimated factor scores for specimens from the factor analysis of all 19 characters. Solid circles represent one or more specimens of *Crotalus h. horridus*; open circles represent specimens of *C. h. atricaudatus*. The X's represent specimens of both. Adult size measurements and postocular stripe (characters SVL, TL, HL, and POS) correlated most closely with factor 1; tail measurements (CS, R, and TL) correlated with factor 2; dorsal scale rows (ADS and DSM) correlated with factor 3; and middorsal stripe (MS) correlated with factor 4.



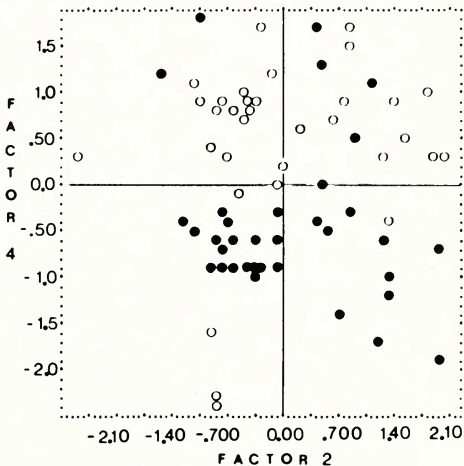
**A**



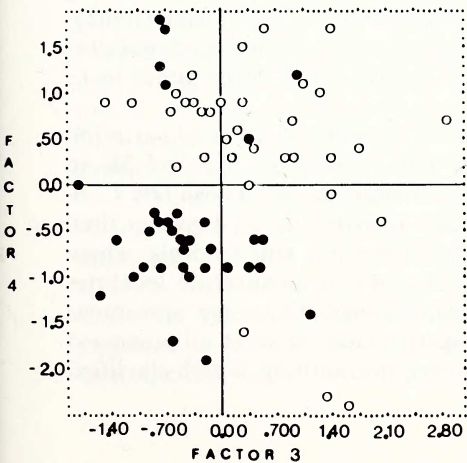
**B**



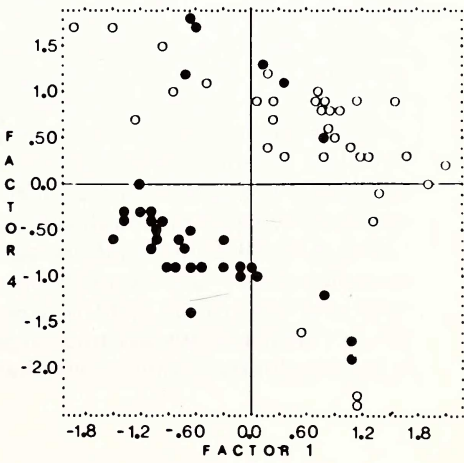
**C**



**D**



**E**



**F**

occur in quadrants one and four, and *C. h. horridus* in quadrants two and three (Fig. 5A). Factor 1 (adult size and postocular stripe), then, appears to differentiate *C. horridus* into two forms. Of those specimens of *C. h. atricaudatus* occurring in the second and third quadrants, only one lacks a postocular stripe, and all are under 1000 mm snout-vent length, the smallest individuals of their group. For example, the specimen of *C. h. atricaudatus* having the largest negative factor 1 score is only 765 mm snout-vent length (probably a subadult). Similarly, those specimens of *C. h. horridus* lying in the first and fourth quadrants are the physically largest individuals of their group. Such large or small individuals, though not typical of their group, can be expected. Factor 2, which includes character R, demonstrates that the ratio of tail length to snout-vent length as an indicator of size is not as reliable as the lengths themselves (factor 1) in distinguishing the two groups. For instance, a large snake having a correspondingly large tail could have the same ratio as a smaller snake, or even one of a different species.

Factor 1 (abscissa) versus factor 3 (ordinate, Fig. 5B) produces a scatterplot much like plot 5A, indicating that factor 3 (dorsal scale rows), like factor 2 (adult tail measurements), is relatively unimportant in differentiating the two subspecies. Factor 1 (adult size) again produces good separation of the two groups in plot 5B with the same individuals lying far to the left or right of their respective groups as seen in plot 5A.

Since factor 2 (adult tail measurements) and factor 3 (dorsal scale rows) have been shown to be unimportant in distinguishing the two groups, the plot of factor 2 versus factor 3 would be expected to demonstrate no clustering, and this is observed in Figure 5C.

In the plot of factor 2 (abscissa) versus factor 4 (ordinate), clustering occurs along the vertical axis, with most specimens of *C. h. atricaudatus* in the first two quadrants and those of *C. h. horridus* in the last two (Fig. 5D). A similar plot occurs for factor 3 versus factor 4, as would be expected (Fig. 5E). Factor 4 (middorsal stripe) therefore appears to differentiate the specimens into two groups: those possessing a distinct middorsal stripe (factor 4 greater than zero, which corresponds to *C. h. atricaudatus*) and those possessing an indistinct middorsal stripe or none at all (factor 4 less than zero, which corresponds to *C. h. horridus*).

Specimens with factor scores outside the normal range of variation for their group were examined more closely in plots 5D and 5E to determine why they clustered with the "wrong" group. Those few *C. h. horridus* that possessed a distinct middorsal stripe (factor 4 greater than zero) were all from localities in North Carolina and Georgia where intergradation might occur. None, in other words, came from localities well to the north of the *C. h. atricaudatus* range. Those few specimens of *C. h. atricaudatus* having a large negative factor 4 score all possessed a faint middorsal stripe, rather than lacked one entirely, which classified

Table 4. Mean character values ( $\bar{x}$ ) and standard deviations ( $s$ ) of all 19 characters for the two subspecies of *Crotalus horridus*. Numbers in parentheses are sample size. One specimen from each subspecies was not included because of unknown sex. M = male, F = female.

	<i>C. h. horridus</i>				<i>C. h. atricaudatus</i>			
	M (14)		F (21)		M (11)		F (22)	
	$\bar{x}$ , s	$\bar{x}$ , s	$\bar{x}$ , s	$\bar{x}$ , s	$\bar{x}$ , s	$\bar{x}$ , s	$\bar{x}$ , s	
ADS	25.29, 1.54	25.38, 0.97	27.54, 1.44	26.14, 1.64				
DSM	23.43, 1.22	23.38, 0.80	24.46, 0.93	24.18, 1.05				
PDS	18.57, 0.76	18.67, 0.73	19.27, 0.65	19.00, 0.62				
VS	163.00, 2.94	166.67, 3.42	167.09, 2.34	169.54, 3.04				
CS	23.64, 1.01	19.81, 1.12	25.54, 2.66	20.23, 1.90				
DCS	1.50, 1.65	1.48, 1.03	3.18, 2.99	1.04, 1.13				
LSL	13.86, 0.86	13.71, 1.10	13.36, 0.92	14.09, 0.92				
RSL	13.86, 1.01	13.33, 0.86	13.27, 0.90	14.00, 0.98				
LIL	14.50, 1.02	14.76, 0.89	15.54, 0.69	15.04, 0.95				
RIL	15.21, 0.70	14.86, 1.01	15.54, 1.29	15.18, 1.14				
BCB	11.14, 3.50	9.14, 3.90	12.54, 3.67	11.82, 2.58				
TCB	0.57, 1.02	0.00, 0.00	1.54, 2.12	0.36, 0.95				
R	0.09, 0.01	0.07, 0.00	0.09, 0.01	0.07, 0.01				
SVL	939.71, 133.96	849.52, 59.77	1049.91, 128.87	1097.91, 116.14				
TL	81.71, 10.62	56.95, 5.52	91.00, 13.03	72.86, 8.17				
HL	42.42, 4.36	39.25, 2.98	47.52, 4.57	48.24, 4.34				
MS	0.29, 0.47	0.10, 0.30	1.00, 0.00	0.86, 0.35				
GC	0.36, 0.50	0.67, 0.48	0.09, 0.30	0.41, 0.50				
POS	0.29, 0.47	0.14, 0.36	0.82, 0.40	0.96, 0.21				

them into the *C. h. horridus* group. Of the properly classified *C. h. horridus* specimens, about 20% possessed an indistinct stripe and 90% lacked one altogether.

Since adult size and middorsal stripe appear to be the most important factors, one plotted against the other (factor 1 versus factor 4) should yield good separation of the groups along both axes, which is the case in Figure 5F. *Crotalus h. atricaudatus* clusters in the first quadrant, and *C. h. horridus* in the third quadrant. The individuals lying outside their respective clusters are a combination of aberrant individuals in the previous plots and have already been discussed.

Characters DSM, PDS, VS, BCB, and TCB were determined to be the combination of variables that best discriminated in the discriminant analysis of the first 13 characters. Pisani et al. (1973) reported characters CS, VS, DSM, and R (in decreasing order of discriminating ability) as the most discriminating in their analysis. Some differences would be expected in light of the different geographical areas sampled. In addition, the method of counting crossbands was different in this study (see

Table 5. Mean character values ( $\bar{x}$ ) and standard deviations ( $s$ ) for each group of *Crotalus horridus* intergrades. All counties are in North Carolina. Burke, Surry, and Wilkes Counties are within the range of *C. h. horridus*; Moore County is within the range of *C. h. atricaudatus*; and Davidson, Randolph, and Stanly Counties lie between the two ranges, as defined by Gloyd (1940). Numbers in parentheses are sample size. One specimen was not included because of unknown sex. M = male, F = female.

	Burke, Surry, Wilkes Counties		Moore County		Davidson, Randolph Stanly Counties		All counties	
	F (4)	$\bar{x}$ , s	M (1)	$\bar{x}$ , s	M (5)	$\bar{x}$ , s	M (6)	$\bar{x}$ , s
ADS	25.00, 0.00		28.00	26.60, 0.55	26.00, 1.05	26.83, 0.75	25.71, 0.99	
DSM	24.25, 0.96		25.00	24.60, 0.89	24.40, 0.97	24.67, 0.82	24.36, 0.93	
PDS	19.00, 0.00		19.00	19.00, 0.00	19.20, 0.63	19.00, 0.00	19.14, 0.53	
VS	167.25, 3.95		163.00	164.20, 2.28	168.20, 3.22	164.00, 2.10	167.93, 3.32	
CS	19.75, 0.50		26.00	23.60, 1.14	19.20, 0.63	24.00, 1.41	19.36, 0.63	
DCS	0.75, 0.50		0.00	1.40, 1.95	1.60, 2.41	1.71, 1.84	1.36, 2.06	
LSL	13.75, 0.96		13.00	13.60, 0.55	14.10, 0.74	13.50, 0.55	14.00, 0.78	
RSL	13.75, 0.96		14.00	14.00, 0.71	14.10, 0.88	14.00, 0.63	14.00, 0.88	
LIL	15.25, 0.50		15.00	15.80, 0.84	16.00, 0.82	15.67, 0.82	15.79, 0.80	
RIL	15.50, 1.00		15.00	15.40, 1.52	15.50, 1.18	15.33, 1.37	15.50, 1.09	
BCB	11.50, 1.73		16.00	11.40, 2.30	10.80, 2.04	12.17, 2.79	11.00, 1.92	
TCB	0.00, 0.00		1.00	0.20, 0.45	0.00, 0.00	0.33, 0.52	0.00, 0.00	
R	0.07, 0.00		0.09	0.09, 0.00	0.06, 0.00	0.09, 0.00	0.06, 0.00	
SVL	957.25, 46.95		983.00	1062.80, 134.64	975.00, 146.12	1049.50, 124.76	969.93, 123.93	
TL	63.75, 4.11		90.00	91.20, 12.56	62.00, 8.33	91.00, 11.24	62.50, 7.25	
HL	42.62, 1.16		44.60	46.90, 4.40	43.95, 4.67	46.52, 4.04	43.57, 3.98	
MS	1.00, 0.00		1.00	1.00, 0.00	1.00, 0.00	1.00, 0.00	1.00, 0.00	
GC	0.00, 0.00		0.00	0.20, 0.45	0.20, 0.42	0.17, 0.41	0.14, 0.36	
POS	1.00, 0.00		1.00	1.00, 0.00	1.00, 0.00	1.00, 0.00	1.00, 0.00	

above). For example, in their study mean body bands ranged from 23.14 to 25.05 among all groups. In our study, body crossbands averaged from only 9.14 to 12.54 (Table 4). The differences in mean tail bands is similar. In our first analysis these characteristics discriminated between the two subspecies, whereas they did not in Pisani et al. (1973); however, their method may have measured an entirely different character variable than the one they intended.

In the discriminant analysis of all 19 characters, 2 of the 6 added characters discriminated. These were HL and MS. Because head length is probably indicative of the total length of the adult snake (Klauber 1938, 1972), it appears that adult size and pattern are important in discriminating between the two subspecies. Dorsal scale rows and number of ventrals also discriminated here, as in Pisani et al. (1973), except that the discrimination was by ADS instead of DSM. Characters BCB and TCB did not discriminate in the second analysis.

In comparing the two analyses, we find that all 19 characters allowed better discrimination. This is evident in the larger eigenvalue (2.989 vs. 1.088), the larger canonical correlation (0.866 vs. 0.722), the smaller Wilks' lambda (0.251 vs. 0.479), and better classification of individuals into the two groups (7% incorrectly classified vs. 16%). In the canonical variable histograms (Fig. 6), separation of the two groups is much better in the analysis of all 19 characters, again showing the importance of size and pattern.

Comparison of the discriminating characters ADS, VS, and HL between nonintergrades and intergrades (Tables 4 and 5) shows that, as expected, the mean character values of the intergrade specimens lie between the mean character values of *C. h. horridus* and *C. h. atricaudatus*, regardless of sex. Since the remaining characters other than MS did not discriminate, their mean values for the intergrade specimens are not expected to be intermediate or even different from the mean values of either *horridus* or *atricaudatus*. Interestingly, all intergrades possessed a distinct middorsal stripe, much like intergrades reported from western localities (Gloyd 1940, Smith 1961, Webb 1970).

Of the three new pattern characters tested in this study (MS, GC, POS; Table 1), POS and, especially, MS were important. None, however, was completely free from subjectivity in measurement. In some cases, the distinction between light- and dark-colored or indistinct and clearly visible was a fine line. Use of old museum specimens, many faded by preservatives, may have induced too much subjectivity, however unintentional. Some dark-colored specimens had a middorsal stripe that had apparently faded to an almost white color, making the stripe unusually conspicuous. Had the specimens been living, the stripe may have been inconspicuous. In other specimens the ground color was faded and difficult to determine. Another problem is the inadequacy of the coding scheme for GC. Gloyd (1940) and others (Wright and Wright 1957, Conant 1975) mentioned that *C. h. horridus* has two color

phases—the typical dark one, as tested for in this study, and a yellow one. There was no possible way, in certain cases, for this study to determine whether a light-colored *C. h. horridus* specimen was truly the yellow phase, as opposed to a badly faded normal dark phase, or the color of a typical *C. h. atricaudatus* specimen. Use of ground color as a discriminating character obviously requires fresh or living specimens and an improved coding scheme.

The evidence presented here suggests that, on the basis of differences in adult size and pattern, two subspecies of *Crotalus horridus* (as described by Gloyd 1940) occur east of the Appalachians. There the races are clearly more distinct than in the western populations. Standard morphological characters alone are not sufficient to separate the two taxa; rather, adult size and pattern differences, in conjunction with the number of dorsal scale rows and ventral scutes, best discriminate *C. h. horridus* from *C. h. atricaudatus*. This combination of size, pattern, and morphological differences needs to be examined in western populations, preferably on living or freshly collected specimens for accurate determination of color and pattern. We feel that the results of our study are preliminary and that a comprehensive study of variation throughout the entire range of *C. horridus* is needed.

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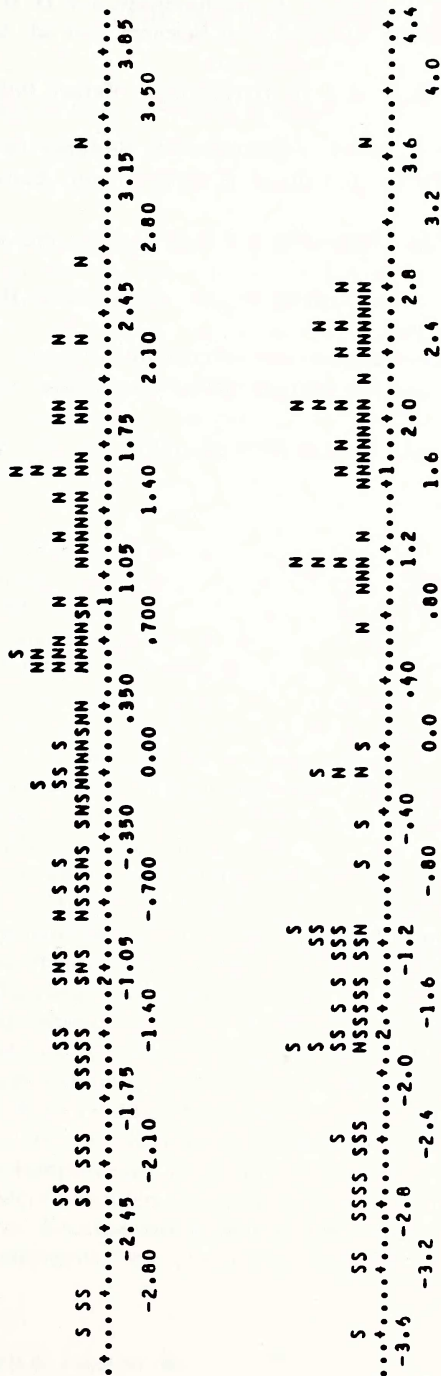


Fig. 6. Histograms of the canonical variable from discriminant analysis of the first 13 characters (top) and from analysis of all 19 characters (bottom). N = a specimen of *Crotalus h. horridus*, S = a specimen of *C. h. atricaudatus*.

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